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STANDING CROP AND NUTRIENT STATUS OF MARION ISLAND (SUB-ANTARCTIC) VEGETATION

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Abstract

The low-altitude vegetation of Marion Island (46° 54′S., 37° 45′E.) is comprised of slope, mire and fjaeldmark plant communities. The standing crop and nutrient status of these communities and a description of the soils underlying them is presented. Marion Island possesses a tundra-type biome and a comparison is made between the standing crop of the island vegetation and those of other circumpolar tundra and alpine vegetations. Slope plant communities support higher standing crops (4 480–6 645 g m^{-2}) than do mire and fjaeldmark communities (2 663 and 2 742 g m^{-2}) respectively. Large quantities (>1 100 g m^{-2}) of dead plant material occur in the island vegetation. The above-ground standing crop (approx. 1 500 g m^{-2}) in the vegetation is larger than those of most northern hemisphere tundra vegetations despite a lower cryptogamic component in the former. The below-ground standing crop of the island vegetation is lower than those of most other tundra vegetation. 1 095 kg ha^{-1} of mineral elements (58% below-ground) accumulates in the island vegetation of which 42% is attributable to nitrogen. Because of the prominence of herbaceous plant species there is a predominance of potassium amongst the ash elements in the plant matter. Deposition of wind-whipped salt-spray on the island surface causes most island plants to contain high concentrations of magnesium and sodium.

Uittreksel

STAANDEOES EN MINERALE STATUS VAN DIE VEGETASIE VAN MARION-EILAND (SUB-ANTARKTIES)

Die laagliggende vegetasie van Marioneiland (46° 54′S., 37° 45′E.) bestaan uit hang, moeras en fjeldmark plantgemeenskappe. 'n Beskrywing van die staandeoes en mineraalstatus van hierdie gemeenskappe, asook 'n beskrywing van die grond word gegee. Die eiland besit 'n tundra-agtige bioom en die staandeoes van vegetasie van hierdie eiland word met ander sirkumpolêre tundra- en alpine-vegetasies vergelyk. Plantgemeenskappe van die hange het 'n hoër staandeoes (4 480–6 645 g m^{-2}) as moeras (2 663 g m^{-2}) en fjeldmark-(2 742 g m^{-2}) gemeenskappe. Groot hoeveelhede dooie materiaal (>1 100 g m^{-2}) kom in die vegetasie voor. Alhoewel daar minder Kryptogamesoorte in die vegetasie van die eiland voorkom as in tundravegetasies van die noordelike halfrond, is die begrondse staandeoes van die eilandvegetasie groter. Die ondergrondse staandeoes van die vegetasie is laer as die van ander tundravegetasies. 'n Totaal van 1 095 kg ha^{-1} minerale elemente (58% onder-

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gronds) word in die vegetasie vasgelê, waarvan 42% aan stikstof toegeskryf word. Die groot aantal kruidagtige plante veroorsaak dat die plantas 'n hoë kaliuminhoud besit. Vanweë groot hoeveelhede soutsproei wat op die eiland voorkom, is hoë konsentrasies magnesium en natrium in meeste plante bepaal.

INTRODUCTION

Marion Island (46° 54′S., 37° 45′E.) has an area of 290 km^2, is volcanic in origin and consists of a coastal plateau and a central mountainous region (highest peak at 1 230 m). Geographically, geologically and biologically it is a true oceanic island (Van Zinderen Bakker Sr., Winterbottom & Dyer, 1971). Being situated in the sub-Antarctic region it is subject to low temperatures, very high rainfall and a high incidence of strong winds (Table 1).

Because of the island's geologically recent origin, its relative isolation and the rigours of the terrestrial environment, the island's biota lacks in species diversity. Only thirty-five vascular plant species occur in the vegetation, of which thirteen are aliens, having been introduced by man (Huntley, 1971). Several score of bryophyte species are present, however, and dense carpets of mosses and liverworts occupy large areas of the island's surface. In addition, many species of lichen occur and algae often form thick mucilaginous mats over the wetter mire areas.

Due to the inclement weather conditions only the lowland areas (below 500 m) support closed plant communities, the mountainous interior being occupied largely by permanent ice- and snow-fields and bare, rocky peaks vegetated only by lichens and a few mosses. An overall, off-shore view of the island presents a bleak, or barren appearance owing to the absence of trees and tall shrubs in the vegetation.

The island consists of two distinctive lava types, a grey pre- and a black post-glacial type. As expected of a young volcanic island, the morphology of any particular area is strongly dependent upon its geological structure and there is a striking contrast between the glaciated areas and those which have subsequently been covered by younger lava flows. These latter areas generally form a hummocky, well-vegetated mosaic of herbfield, mire and fjaeldmark, depending upon local variation in slope, wind exposure and drainage. The smooth topography of the glaciated areas, however, offers little protection from wind erosion and consequently supports a sparser flora, mostly open fjaeldmark on the ridges with mire vegetation occupying the numerous ill-drained basins. Black lava flows form approximately 80% of the island's surface and estimates of the standing crop and nutrient status of the plant communities occupying these flows are presented in this paper. An area of approximately 1,8 ha (altitude *c.* 50 m) which contained typical representatives of the plant communities of the island's eastern coastal plain formed the intensive study site for both investigations.

In several aspects Marion Island possesses a tundra-type biome. Restrictively, *tundra* is defined as areas where the average annual temperature is below 0°C and permafrost occurs. Defined in a wider sense, however, tundra includes all areas

TABLE 1.

Climatic data for Marion Island (after Schulze, 1971).

	Jan.	Feb.	Mar.	Apr.	May	June	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Year
Frequency of days with gales (10 years' record)	8,7	6,2	6,5	8,0	8,6	9,5	10,7	10,3	11,4	8,4	8,4	10,1	106,8
Mean monthly air temperatures, °C (12 years' record)	6,7	7,3	7,2	6,0	4,8	4,0	3,6	3,2	3,3	4,3	5,1	5,8	5,1
Mean monthly relative humidities, % (12 years' record)	81	83	83	84	83	83	84	83	83	81	81	81	83
Mean monthly precipitation, mm (15 years' record)	222	207	225	238	249	232	231	185	201	165	196	225	2 576
Mean daily total radiation reaching surface in cal. cm^{-2} day^{-1}	495	435	316	196	142	—	113	181	273	416	494	508	±304

where the temperature is too low or precipitation and wind too great for a natural forest vegetation to develop (Wielgolaski, 1972a). Thus oceanic moorland areas and some mountainous regions, which have somewhat higher annual temperatures, are also included. A comparison of the standing crop and nutrient status of Marion Island vegetation with that of other tundra vegetations is provided in the discussion.

TERMINOLOGY

Biomass refers to the total amount of living plant organic matter and is divided into *above-ground biomass* and *below-ground biomass*. *Dead organic matter* refers to dead plant material and is similarly divided into above-ground and below-ground components. The latter does not include the decomposed or humified organic constituents of the soils and peats. *Above-* and *below-ground standing crops* are the sums of the appropriate biomass and dead organic matter components, while the term *total standing crop* refers to the sum total of the above and below standing crops.

The magnitude of these various standing crop components are presented on a dry-weight basis and are expressed as g m^{-2}.

METHODS

1. *Harvest sampling*

The standing crop estimates reported in Table 4 reflect the average maximum standing crops attained by the plant communities in the study site during the 1971–2 and 1973–4 growing seasons.

In each plant community the average aerial cover of the overall vegetation and of each species was found using a series of 50 × 50 cm quadrats. Quadrat samples for harvest were taken separately for each species from areas within the plant community containing between 90–100% aerial cover of the particular species. The living and dead plant material was clipped to soil-level and all litter also collected. The harvested material was sorted into categories of plant organs (flowers, stems, leaves, sporulating fronds, etc.) and oven-dried at 105°C to constant weight. The oven-dry weights of these organs were readjusted to the average percentage cover of the particular species within the community. The dried harvested material was kept for chemical analysis.

The size and number of sampling unit replicates used in the harvesting depended upon that needed to obtain a reliable (< 25% coefficient of variation) estimate of the above-ground standing crop of the particular species. For most species 4–6, 0,1 m^2 sampling units were used. The extremely uniform structure of pure stands of *Blechnum penna-marina* (Poir) Kuhn and of cushions of *Azorella selago* Hook.f. enabled similarly reliable estimates of the aerial standing crops of these two species to be derived from 4–6, 50 cm^2 circular sampling units.

Below-ground standing crop was sampled at each clipped site using a 50 cm^2

core borer which removed a plug of earth with roots and rhizomes to a depth of 50 cm. These were washed free of soil and organic debris, sorted into species and the visibly dead material separated from the living material. The separate components were oven-dried, weighed, and the oven-dry weights readjusted in the same manner as those of the aerial plant material. Because of the difficulties encountered in distinguishing the living from the dead underground material of some species, these two components are not reported separately in this account but rather a composite figure (below-ground standing crop) is presented.

The relative areas occupied by each community on the surface of the intensive study site are not representative of their proportions in the black lava regions of the island's eastern coastal plain as a whole. In order to provide an estimation of the overall vegetation standing crop of these regions, an assessment of the true extent of each community within the larger area had to be made. Accordingly, diagonal traverses of a 10 km^2 area on the eastern coastal plain of the island were marched on fixed compass bearings and the number of footfalls, or footsteps in each plant community encountered on the marches was recorded, i.e. each footstep was regarded as a point. Points were 75 cm apart and this distance was kept constant by a piece of string tied between the walker's feet. This modified step-point method proved to be a rapid means of assessing the relative areas occupied by the different plant communities.

2. *Chemical analyses: plant material*

Ash elements: 1 g of the harvested plant material was ashed at 450°C for 1½ hours in a muffle furnace, the ash dissolved in concentrated HNO_3 and the acid evaporated off. The ash was replaced in the furnace for 20 minutes at the same temperature and the resultant residue taken up in hot, dilute HNO_3. The concentrations of calcium, magnesium, sodium, potassium and iron in the ash extract were determined by atomic absorption spectrophotometry and the amount of phosphorus by the method of Kitson and Mellon (1944).

Nitrogen was measured according to the method used in the determination of the total nitrogen content of soils. Although losses of N from plant tissue dried at 105°C have been reported in the literature, no significant differences were found in the nitrogen contents of replicate samples of most Marion Island plant species dried at 60°C, 80°C or 105°C. Tissue inherently high in nitrogen, however, exhibited slightly lower measured nitrogen values when dried at 60°C rather than 105°C, probably due to enhanced enzymatic breakdown of tissue proteins with subsequent volatilization of the newly released N fractions during the slower killing of the tissue at the lower temperature. Green tissue dried at 105°C retained its colour during the drying period and reached constant weight in 12–48 hours against 36–72 hours needed for similar tissue at 60°C. The latter never retained its green colour during the drying period. High humidity of the laboratory air on the island was almost certainly responsible for the retarded drying of the plant tissue at 60°C.

3. *Chemical analyses: soils*

Inorganic nitrogen was determined on fresh, undried soil samples. All other analytical procedures were performed on air-dried, sieved (2 mm) soil samples excepting for organic carbon determinations which were made on ground (0,2 mm) samples. Results of the determinations are expressed per unit oven-dry weight of the soils.

Total nitrogen content was determined according to the regular macro-Kjeldahl method of Bremner (1965a) excepting that a steam distillation method was employed for the determination of ammonia in the digest. *Inorganic nitrogen:* the MgO-Devarda Alloy steam distillation method whereby KCl extracts of fresh soils were analysed for ammonium and nitrate-nitrogen (Bremner, 1965b), was used. *Organic carbon* was measured by the Walkley-Black method (Allison, 1965), modified slightly in that a 2N dichromate solution was employed. Organic carbon values reported in Table 3 are uncorrected for soil chloride content. *Total phosphorus* was determined by the ignition method of Legg and Black (1955) except that the ignited soils were taken up in 10 N HNO_3 rather than in conc. HCl. The concentrations of P in the extract were determined according to the method of Kitson and Mellon (1944).

Soil cation exchange capacity was determined by saturating the soils' adsorption complex with Ca^{2+} by equilibrating 5 g soil samples with 0,1 M $CaCl_2$. After removal of the free calcium ions in the soil solution with rinses of isopropanol the saturating Ca^{2+} ions were displaced using 1 N $NH_4 NO_3$ in 60% ethanol solution and the concentration of these ions in the leachate measured by atomic absorption spectrophotometry.

Total exchangeable cations: A 5 g soil sample was washed by filtering through small portions of 60% ethanol and the adsorbed cations then displaced using a 1 N NH_4Cl in 60% ethanol solution. The concentration of cations in the leachate was measured by atomic absorption spectrophotometry.

Soil pH was measured in a soil suspension of 1 part soil : 2 parts 0,01 M $CaCl_2$ solution (W : W) and *soil water content* determined by drying fresh samples of soil at 105°C to constant weight.

DISCUSSION AND RESULTS

1. *Description of the vegetation and soils*

The younger black lava areas of the island coastal plain are typified morphologically by being extremely hummocky and, except for the exposed rocky ridges and plateaux, well vegetated (Fig. 1). Several distinct plant communities occur within the black lava areas. These may be grouped into three categories, viz. (i) vegetation of the slope complex, (ii) mire vegetation, and (iii) vegetation of the exposed rocky plateaux, or fjaeldmark.

(a) *The slope complex*

Five plant communities occupy the numerous slopes of the hummocks and ridges of the island's low-altitude black lava areas. A summary of their floristic composition is provided in Table 2 while a more detailed description of their nature and distribution may be found in Huntley (1971).

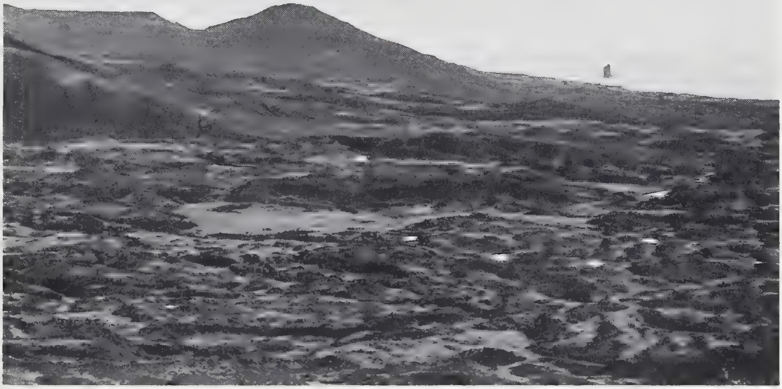

Fig. 1.

Overall view of the hummocky, low-lying north-eastern coastal plain of Marion Island. Distance from photographer to rock in sea is approx. 7½ km.

The soils under the slope plant communities are remarkably similar regarding their profile characteristics. Slope soils overlie porous loose-rock and scoria deposits and, except for those occurring directly in drainage lines, are consequently well drained. The chemical status of the slope soils differs according to the vegetation cover, however, and chemical data for the upper horizons of these soils is presented in Table 3.

(i) *Blechnum penna-marina* fernbrake community.

The dominant cover of slopes protected from the icy southern and south-western winds is that of a thick continuous carpet of the fern *Blechnum penna-marina* which may occupy several hundred square metres of such leeward slopes (Fig. 2). Cushions of *Azorella selago* and tussocks of the grass *Poa cookii* Hook.f. are frequent in the otherwise uniform fern carpet and, where rocky outcrops occur, the rosaceous shrub *Acaena magellanica* (Lam.) Vahl. occurs. Other vascular plant

Table 2.

Percentage aerial cover values of component species in the plant communities occurring on the black lava flows of the Marion Island eastern coastal plain.

Plant community	*B. penna-marina*	*Poa cookii*	*A. selago*	*A.*(1) *magellanica*	*A.*(2) *magellanica*	Bryophytes	Algal mats	Other	Total
Slope complex									
B. penna-marina fernbrake	79	9	15	3	tr	tr	nil	tr	106
Open, scrub community	42	8	31	15	1	nil	nil	nil	97
A.(1) *magellanica* drainage line	24	1	3	75	nil	80	nil	tr	183
P. cookii, A. selago crest	11	57	36	2	2	tr	nil	nil	108
P. cookii tussock grassland	11	37	11	43	nil	85	nil	2	189
Mire complex									
A.(2) *magellanica* mire	nil	nil	tr	nil	49	75–90	0,5–1	12(3)	97
Fjaeldmark									
A. selago fjaeldmark	9	nil	27	nil	16	1	nil	tr	53

(1) *Acaena magellanica*
(2) *Agrostis magellanica*
(3) Including *Uncinia dikei (8%), Juncus scheuchzerioides (4%).*
tr = trace, less than 0,5%.

TABLE 3.

Chemical status of the horizons containing living roots in the soils under Marion Island plant communities

Plant community	N	cm Depth	pH	% Water	% saturation of C.E.C.					% Org.–C	% Total–N	% Total–P	mg/100 g soil	
					Ca	Mg	Na	K	Total				NH_4–N	NO_3–N
SLOPE COMPLEX														
B. penna-marina fernbrake	8	0–18	4,3	715±67,0	21±5,2	40±2,2	4±0,8	7±2,1	72±5,4	43,8±1,33	2,18±0,161	0,74±0,195	tr.–1,6	0,0–tr.
Open scrub community	4	0–10	N.D.	325±45,9	13±2,9	14±2,1	4±0,9	1±0,5	31±5,4	12,7±3,16	1,24±0,310	0,52±0,093	tr.–0,9	0,0–tr.
A. magellanica drainage line	6	0–45	4,2–4,7	1 002±275,0	26±1,1	32±9,0	4±1,9	2±1,0	65±10,8	42,9±10,66	2,50±0,442	0,66±0,224	tr.–2,9	0,0–tr.
Poa cookii, A. selago crest	4	0–17	4,3–4,4	450±328,8	11±4,5	14±6,8	5±2,3	2±2,3	31±15,8	23,9±16,20	1,63±0,733	0,56±0,480	tr.–1,7	0,0–tr.
Poa cookii tussock grassland	8	0–50	4,0–4,1	360±23,2	14±1,2	13±3,0	5±2,2	1±0,5	34±4,1	25,0±4,73	1,66±0,298	1,55±0,456	0,9–8,4	0,0–1,0
MIRE COMPLEX														
Agrostis magellanica mire	10	0–20	4,2	1 667±199,1	5±1,5	13±0,5	5±0,7	3±1,0	26±1,5	48,1±4,93	2,34±0,420	0,60±0,491	2,4–6,5	0,0–0,7
FJAELDMARK														
A. selago fjaeldmark	4	0–10	N.D.	217±168,4	3±2,1	9±3,4	3±1,9	2±3,3	17±5,9	6,0	0,73	0,42	0,0–0,5	0,0–tr.

N = number of determinations.
Values expressed as ranges or as means ± standard deviations.
N.D. = not determined.
tr. = trace (< 0,5 mg/100 g soil).

species account for less than 1% of the vegetation cover (and standing crop) of this plant community which, following Huntley (1971), is termed *fernbrake* vegetation. The moss *Rhacomitrium lanuginosum* (Hedw.) Brid. and the liverwort *Plagiochila crozetensis* Kaal., the latter usually associated with *A. selago* cushions, also occur but the non-vascular component commonly accounts for less than 0,5% of the total vegetation cover of fernbrake communities.

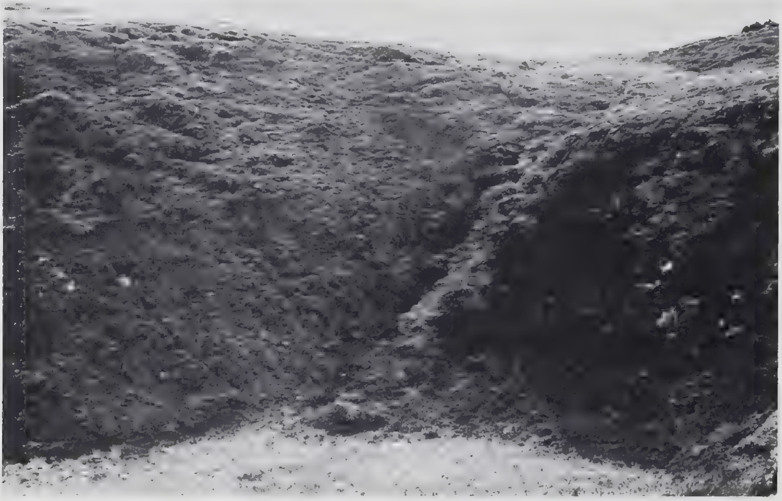

FIG. 2.
Blechnum penna-marina fernbrake community on an east-facing slope. A narrow drainage line connecting two mire areas and dominated by *Acaena magellanica* is prominent. Height of slope approx. 20 m.

(ii) Open scrub community.

Slope areas offering less protection from the wind, or which are occupied by a large number of rocky outcrops breaking the soil cover, support a stunted *Blechnum penna-marina* vegetation cover in which there is an increased importance of *Azorella selago* and *Acaena magellanica* (Fig. 3). The aerial cover of the vegetation of these areas is indicated in Table 2 as being almost 100%. This is due to the increased *A. magellanica* canopy over the *Blechnum* fronds and to a greater expanse of *A. selago* cushions, on which the other component species often occur epiphytically. Basal vegetation cover of these areas is much lower than that of fernbrake areas and the vegetation has an open, scrubby appearance. Although the term *scrub* is most usually associated with arboreal vegetation, it has been used in describing low-growing, sub-climax vegetation covers (Ashby, 1969) and in this account the term *scrub community* is used in referring to the open vegetation of the exposed or rocky-slope areas.

The soils under fernbrake and scrub communities are similar in profile characteristics excepting that the latter soils are somewhat shallower. A fibrous mat of *B. penna-marina* rhizomes, fronds and litter merges with a black or dark-brown humic A horizon, the upper regions of which contain dead plant remains and live roots. A well-developed B horizon occurs beneath this A horizon, changing from dark-brown through yellow-brown to a red-orange colour with increasing depth. This latter colour represents the zone of sesquioxide enrichment and an iron pan is most often present, usually immediately above the parent rock.

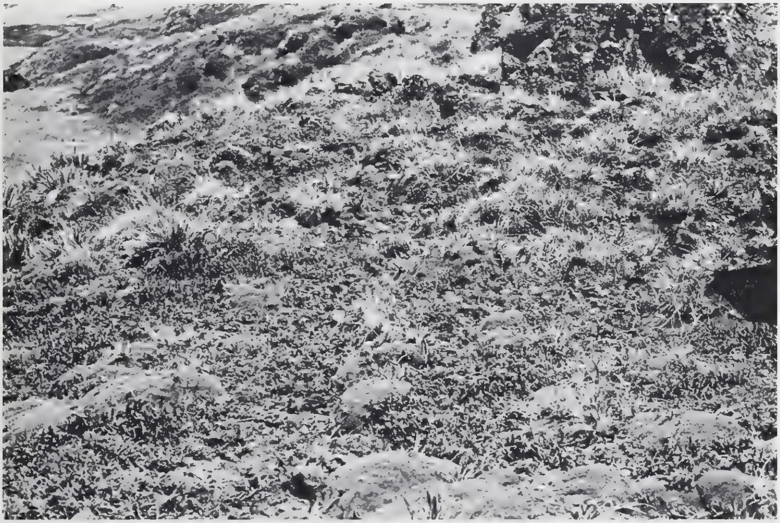

FIG. 3.

Open scrub community of *Blechnum penna-marina, Azorella selago, Poa cookii* and *Acaena magellanica*. Distance of *A. selago* cushions in foreground to large rock at upper right is approx. 10 m.

The upper soil horizons under fernbrake communities are more organic and possess higher water and total nitrogen contents than do those under scrub communities (Table 3). The lower water retention of the scrub soils allows for more intensive leaching of nutrients, possibly explaining the lower percentage base saturation of these soils.

All non-biotically influenced slope soils possess low contents of inorganic nitrogen, predominantly in the ammonium form. Negligible concentrations of nitrate nitrogen occur, as might be expected under the low pH-low temperature soil régime.

(iii) Wet, *Acaena magellanica*-dominated drainage line community.

Depressions and drainage lines in the slope areas are invariably occupied by a dense canopy of *Acaena magellanica* interspersed with long etiolated fronds of *Blechnum penna-marina* and understoreyed by a luxuriant growth of the moss *Brachythecium rutabulum* (Hedw.) B.S.G. (Figures 2 + 4). The vegetation of these drainage lines and depressions is equivalent to the *Acaena decumbens* (= *A. magellanica*, Walton, pers. comm.) – *Tortula robusta* Hook. et Grev. communities of sheltered depressions attracting run-off water in slope areas on South Georgia (Walton, 1973). Although rapid flow of water occurs through the soils under Marion Island drainage line communities, the deeper layers of the humus-rich, clayey B horizon of these soils are often anaerobic. The soils are very wet and the water-table seldom more than a few cm below the surface.

The percentage base saturation of drainage line soils is less than that of surrounding soils under fernbrake, largely because of lower contents of magnesium in the former (Table 3). This may be due to the ease with which magnesium is leached from colloidal adsorption surfaces. The increased importance of calcium in the cation suite of drainage line soils is reflected by increases in the content of this element in the leaves of *Acaena magellanica* plants growing in these soils (see section 3a).

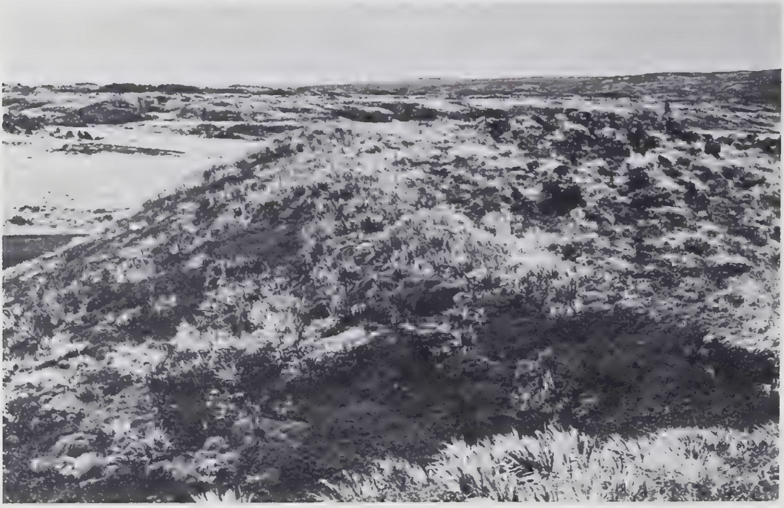

FIG. 4.

Poa cookii – *Azorella selago* community on crest of slope. Wet depression dominated by *Acaena magellanica* prominent in foreground. Fjaeldmark at right and mire vegetation in background at left. Width of crest community approx. 5 m at widest point.

(iv) *Poa cookii – Azorella selago* slope-crest community.

On the exposed crests of slopes supporting a fernbrake community a narrow bank of *P. cookii* understoried by large cushions of *A. selago* often occurs (Fig. 4). Both these species are tolerant of cold air and cold soil (Huntley, 1971) and this may be the reason for their association in this distinctive band, which is seldom more than 3–5 m wide, on the exposed crests of the slopes.

The soil profiles under the *crest* communities are essentially similar to those under fernbrake excepting that the lighter-coloured A horizon of crest soils is less humic and that larger quantities of scoriae occur in the deeper soil horizons. The content of organic carbon, total nitrogen, total phosphorus and adsorbed cations is lower in these soils than in those under fernbrake (Table 3).

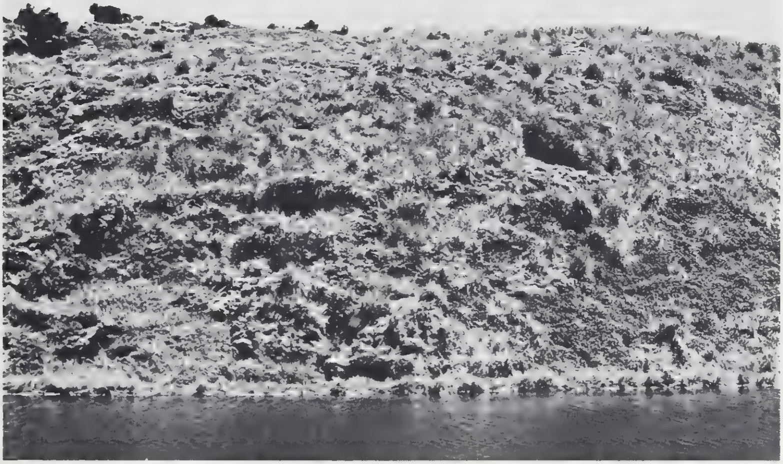

Fig. 5.

Poa cookii tussock grassland on inland, east-facing slope. Dense *Acaena magellanica* cover is obscured by the long leaves of the grass. Height of slope approx. 20 m.

(v) *Poa cookii* tussock grassland.

In many well-drained, protected slope areas the *Blechnum penna-marina* carpet is replaced by a dense plant cover comprising *Acaena magellanica* codominant with luxuriant swards of *P. cookii* (Figures 5 + 6). A dense understorey of *Brachythecium rutabulum* occurs and *Azorella selago* and *B. penna-marina* are common throughout this community, which has been termed *inland tussock grassland* by Huntley (1971) and which is invariably undermined by numerous burrows of small petrel and prion species. The high inorganic nitrogen contents of the soils under inland tussock grassland communities (Table 3) evidences the influence of the birds on the nutrient status of these soils. In relation to their relatively low organic carbon values, the total phosphorus content of tussock grassland soils is also high, possibly indicating enrichment in inorganic phosphorus by the bird guano. This is substantiated by the effect which these birds have on the nutrient status of the plants growing in the inland tussock grassland communities (Smith, 1976).

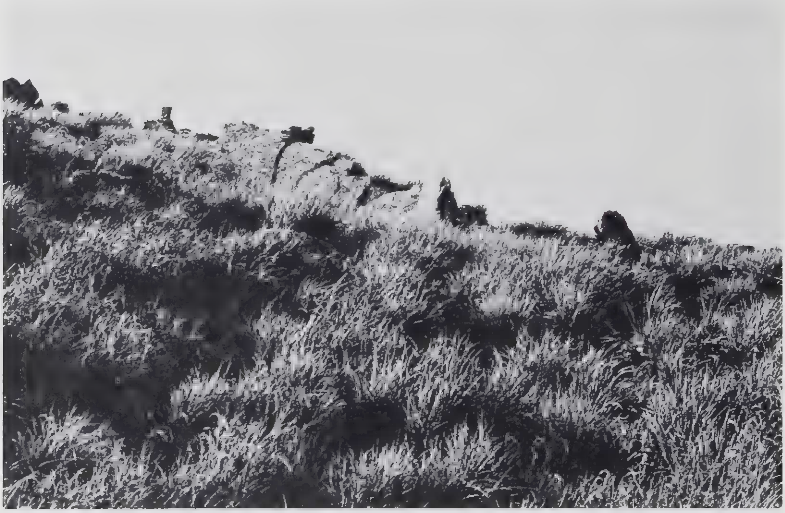

Fig. 6.
Close-up of *Poa cookii* tussock grassland. *Acaena magellanica* cover visible in shadows of grass tussocks. Height of tussocks approx. 60 cm.

(b) *The mire complex*

The topography formed by the younger lavas as well as the extremely porous and *blocky* structure of these lavas is of such a nature that very few stream courses exist in areas covered by them. Considering the high rainfall, considerable amounts of water must reach the sea via underground drainage. A characteristic feature of the hummocky topography is, in fact, the numerous small bogs between the humps in which subsurface drainage from the surrounding slopes is ponded.

In many such areas the bogs have been succeeded by soligenous mires (Fig. 7). The dominant vascular plant cover of these mires is an open canopy of the grass *Agrostis magellanica* Lam. under which numerous individuals of *Uncinia dikei* Nelmes and *Juncus scheuchzerioides* Gaud. usually occur (Table 2). Several bryophyte species often form a dense carpet under the *A. magellanica* canopy; the most common of these are *Drepanocladus uncinatus* (Hedw.) Wernst., *Rhacomitrium languginosum* and *Plagiochila crozetensis*. In extremely wet regions a dense carpet of *Blepharidophyllum densifolium* (Hook.) Angstr. Arnell develops.

The water-table is almost continuously at the surface within the mire areas. Peat formed in these areas is deep and amorphous and mineral horizons seldom occur within the profile.

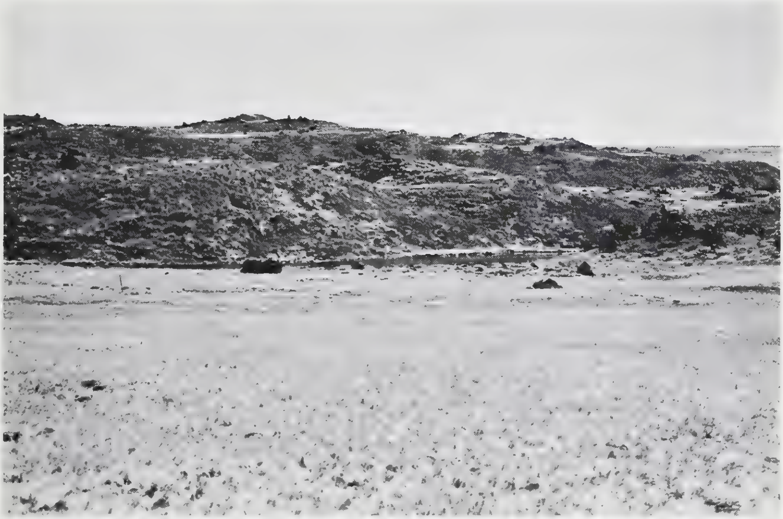

Fig. 7.
Agrostis magellanica mire community with slope complex in background. Distance to near edge of lava lakelet approx. 60 m.

The ammonium nitrogen status of mire peat is fairly high in comparison with that of the slope soils (Table 3), although not as high as those of many other peaty soils where values of 40–60 mg 100 g $soil^{-1}$ have been reported (Harmsen and Kolenbrander, 1965). These relatively high values for ammonium nitrogen in the island peat may be due to the breakdown of labile organic substances during the distillation procedure, despite precautions employed against this (filtration of the soil extract, use of MgO and short distillation times). It is of interest, however, that all peat samples exhibiting the higher values in the range of ammonium nitrogen contents reported in Table 3 occurred under a thick gelatinous algal mat containing *Nostoc commune* Vaucher (although the presence of such a mat did not always imply a high ammonium nitrogen content). Croome (1973) has shown that *N. commune* fixes significant quantities of atmospheric nitrogen in the island mires and the data in Table 3 indicate that this fixation serves to enrich these mires in reduced nitrogen.

(c) *The exposed rocky plateaux: fjaeldmark communities*

Exposure to wind limits the growth of most plant species on the rocky plateaux. *Azorella selago, Agrostis magellanica* and a few scattered, stunted individuals of *Blechnum penna-marina* form the vegetation cover of these areas (Table 2). In areas completely exposed to the wind, the total plant cover seldom exceeds 5%. These are the true fjaeldmark, or wind desert, communities and occur mainly above the 200 m contour (Huntley, 1971). On the rocky plateaux of lower-lying areas, however, the cushions of *A. selago* are large and very numerous, supporting many epiphytic individuals of *A. magellanica* (Figures 4 + 8). The percentage aerial cover of the vegetation in such areas is between 50% and 60% and basal cover may be as high as 50%.

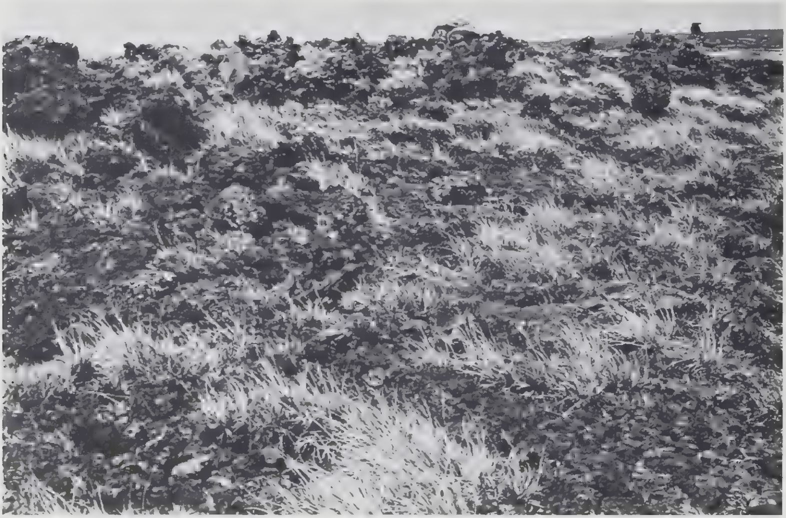

Fig. 8.

Rocky, exposed plateaux supporting a relatively well-vegetated fjaeldmark community typical of the low-lying island regions and dominated by *Azorella selago* and *Agrostis magellanica*, the latter mostly epiphytic on cushions of the former. Distance to rocky outcrops in background approx. 15 m.

Soils developed under fjaeldmark vegetation are skeletal, gravelly loams of a shallow nature. Where plants are growing at the immediate surface the amount of soil organic matter in the top few cm may be high owing to the slow breakdown of the plant remains in the low temperatures prevalent in fjaeldmark areas. Fjaeldmark soils are, however, generally much less organic than are those of the mire

TABLE 4.
Standing crops of Marion Island plant communities.

Plant community	standing crop component (g m^{-2})						Total Stand Crop	Surf. Area Occup.*	S.C. in Average Hectare**
	Above-ground					Below-ground S.C.			
	Biomass Vasc.	Biomass Cryp.	Total	Dead O.M.	Total S.C.				
SLOPE COMPLEX									
Fernbrake community	568±79	tr	568	1 557±322	2 125	3 984±684	6 109	18,0	10 996
Open scrub community	438±63	tr	438	1 580±208	2 018	2 462±441	4 480	21,6	9 677
Acaena drainage line	727±92	224±94	951	528±107	1 479	3 607±572	5 086	0,3	153
P. cookii, A. selago crest	804±117	tr	804	3 654±1 086	4 458	2 001±227	6 459	1,0	646
P. cookii tussock grassland	778±134	230±49	1 008	1 649±225	2 657	3 988±898	6 645	0,6	399
MIRE COMPLEX									
Agrostis magellanica mire	117±29	219±82	336	303±69	639	2 024±421	2 663	37.4	9 960
FJAELDMARK									
Azorella selago fjaeldmark	238±36	tr	238	1 541±183	1 779	963±224	2 742	20,9	5 731

*percentage
**kg ha^{-1}

TABLE 5.

Standing crops of sub-Antarctic and other tundra-type vegetations.

Tundra-type Location and Vegetation	Standing Crop Component (g m^{-2})						
	Above-ground					Below-ground Total	Total in S.C
	Biomass			Dead O.M.	Total Above		
	Vasc.	Cryp.	Total				
Sub-Antacrtic							
Marion Island (1972, 1974)							
Mosaic of slope, mire and fjaeldmark vegetation	306	84	390	1 105	1 495	2 262	3 757
Marion Island (1969)[1]							
Fernbrake community			799				
Tussock grassland			449				
Agrostis mire			329				
Macquarie Island[2] (54° 30′ S.)							
Pleurophyllum hookeri herbfield			760				
Poa foliosa tussock grassland	920		920*	3 300*	4 220*	8 400*	12 620*
South Georgia (54° 16′ S.)							
Acaena magellanica wet depression[3]	1 117	221	1 338	519	1 857	7 536	9 393
Festuca erecta grassland[4]	424	170	594	1 654	2 248	1 682	3 930
Sub-Arctic and Low-Arctic							
Koryak National Territory, U.S.S.R.[5]							
Mosaic tundra of sedges, mosses, lichens and shrubs	218	261	479	521	1 000	2 307	3 307
Hillocky tundra of sedges, mosses, lichens and shrubs	250	241	491	410	901	2 387	3 288
Vorkuta Region, U.S.S.R.[6]							
"Typical" tundra of low shrub, mosses	188	319	507	366	873	6 226	7 099
Woody sub-Arctic shrub-dwarf shrub tundra	817	1 345	2 162	24	2 186	15 016	17 202
Abisco (68° 15′ N.)[7]							
Calamagrostis purpurea grassland			234				
Calamagrostis purpurea grassland max.			458				
Sedge swamp			242				
Sedge swamp max.			373				
Arctic							
Devon Island Truelove Lowland (75° 40′ N.)[8]							
Sedge meadows, beach meadows and rock outcrops	79		79*	143*	222*	1 090*	1 312*
Bolshoy Lyakovskiy Island, U.S.S.R.[5]							
Hummocky tundra of sedges, grasses, shrubs and mosses	71	115	186	69	255	821	1 076
Polygonal moss and forb tundra	49	70	119	61	180	352	532
Barrow, Alaska (71°20′ N.)[9]							
Predominantly graminoid-species vegetation					112–266	1 520–2 185	1 778–2 438

* excluding cryptogamic component.

1. Huntley (1972a).
2. Jenkin and Ashton (1970).
3. Walton (1973).
4. Greene, Walton and Callaghan (1973).
5. Rodin and Bazilevich (1967).
6. Bliss (1973).
7. Pearsall and Newbould (1957).
8. Calculated from the data of Bliss and Kerik (1973), Muc (1973) and Svoboda (1973).
9. Dennis and Johnson (1970).

Alpine							
Mount Washington[10]							
Carex bigelowii meadow			203–208				
Rush-dwarf heath meadow			81–109				
Mts Wyoming[10]							
Carex scapulosum-Deschampsia caespitosa meadow			112				
Koryak National Territory, U.S.S.R.[5]							
Alpine shrub tundra	80	25	105	54	159	1 244	1 403
Non-tundra type							
Osage, U.S.A.[11]							
Mixed tall-grass species prairie	274		274	230	504	1 184	1 688

10. Bliss (1962).
11. Sims and Singh (1971).

and slope complexes (Table 3). The soils are also very poor in base content, due possibly to rapid percolation of incoming rainfall through these soils because of their low water-retention capacity.

2. *Standing crops of the plant communities*

The standing crop values of the various plant communities at the time of maximum above-ground biomass and the contribution of these communities, in relation to their proportionate representation, to the average standing crop of one hectare of the black lava areas of the island's eastern coastal plain are presented in Table 4. In Table 5 a comparison of this average standing crop with those of other circumpolar tundra and alpine vegetations is provided.

(a) *The slope complex*

The plant communities of the slope complex support far higher standing crops of plant matter than do those of the mire and fjaeldmark areas (Table 4). This is due to the higher above-ground biomass and below-ground standing crop of the slope communities and is in accordance with the results of other studies on hummocky and hillocky tundra areas (Rodin and Bazilevich, 1967).

The estimate of 568 g m^{-2} for the above-ground biomass of Marion Island fernbrake vegetation is substantially lower than the corresponding value (799 g m^{-2}, Table 5) reported by Huntley (1972a) for April 1969. This earlier estimate was based upon a fernbrake stand possessing a high (95%) cover of *Blechnum penna-marina* with *Azorella selago* contributing only 5% towards the total aerial vegetation cover. Although such well-developed stands do occur on slopes offering complete protection from southern winds, the average *B. penna-marina* cover of typical fernbrake areas is usually much lower and *A. selago*, a species exhibiting a low above-ground biomass, is of greater importance in such areas.

Expectedly, the open, stunted plant growth of the exposed scrub slopes causes these areas to exhibit the lowest above-ground biomass and overall standing crop of all the communities of the slope complex. An examination of the floristic composition of the vegetation of these scrub areas (Table 2) demonstrates the importance of *A. selago* in the standing crop of this vegetation. The cushion habit of this species allows negligible dissemination of the produced leaf and stem material once this has died even though the cushions are commonly found in areas subjected to long periods of gale-force winds. Considering that some cushions on Marion Island are estimated to be over 100 years old (Huntley, 1972b), large quantities of dead material can accumulate and this contributes substantially to the overall vegetation standing crop. Huntley *(l.c.)* considers that *A. selago* has the highest standing crop of all the vascular plants on the island. *Azorella* cushions occupy 31% of the scrub areas and without the dead material contained in them these areas would support a very much lower standing crop than is indicated in Table 4.

Previous workers have shown that extremely large amounts of dead plant material accumulate in the swards and tussocks of sub-Antarctic and Antarctic grasslands. The graph presented by Jenkin and Ashton (1970) indicates that approximately 80% of the above-ground standing crop of *Poa foliosa* Hook.f. grassland on Macquarie Island consists of dead *P. foliosa* while Greene, Walton and Callaghan (1973) found that 71% of the above-ground standing crop of a *Festuca erecta* D'Urv. grassland community on South Georgia was accounted for by dead material, predominantly that of *F. erecta*, despite the fact that living material of this species contributed only 8% towards the total standing crop of the vegetation. Data reported by Edwards (1973) indicate that dead plant material constitutes between 40% and 90% of the above-ground standing crop of a closed *Deschampsia antarctica* Desv. sward on Signy Island (Maritime Antarctic).

The current study on Marion Island supports these previous observations and large amounts of dead (and living) plant matter accumulate in the perennial tussocks of the grass *Poa cookii*. The dominance of this species, along with that of *A. selago*, in the narrow bands of vegetation on the crests of slopes causes these areas to support by far the highest above-ground standing crop (4 458 g m^{-2}) of all the island plant communities, despite the absence of a significant bryophyte stratum beneath the *Poa* canopy. This value is similar to that reported by Jenkin and Ashton (1970) of 4 220 g m^{-2} for the above-ground standing crop of Macquarie Island tussock grasslands (Table 5), considering that the bryophyte component was not included in their estimate. Because of the low below-ground standing crop, however, the total standing crop of the Marion Island slope-crest communities is approximately half that of the Macquarie Island tussock grasslands.

Many large perennial roots and rhizomes are developed by *Acaena magellanica* plants and communities in which this species is an important constituent exhibit high below-ground standing-crop values (Table 4). This is in accordance with similar observations on *A. magellanica*-dominated communities on South Georgia (Walton, 1973; Greene, *et al.*, 1973). The luxuriant growth of *Brachythecium rutabulum* which occurs under the *Acaena* canopy on Marion Island also adds substantially to the overall vegetation standing crop in these areas.

The above-ground vascular biomass of wet depressions dominated by *A. magellanica* on South Georgia (Table 5) is approximately 50% greater than that of the depression and drainage line communities on Marion Island. This reflects the lower percentage cover of *A. magellanica* in the Marion Island communities. *Blechnum penna-marina*, a species possessing no above-ground perennial tissue, constitutes roughly a quarter of the vegetation cover in these communities, in contrast to the complete dominance of *Acaena* in the South Georgian communities (Walton; *l.c.*). The underground standing crop of the South Georgian communities is twice that of the corresponding communities on Marion Island. The total standing crop in the former is therefore extremely high, ranking with that of many sub-Arctic shrub tundras and with that of Macquarie Island tussock grassland.

The importance of the three species, *Poa cookii, Azorella selago* and *Acaena magellanica* in the tussock grassland of the slope complex causes this community to exhibit the highest total standing crop of all Marion Island plant communities. The above-ground biomass of tussock grassland (1 008 g m^{-2}) is more than double that reported by Huntley (1972a) and is considerably higher than that of a similar, well-developed *Festuca erecta-Acaena magellanica* community on South Georgia (Greene, *et al.*, 1973).

The floristic composition of tussock grasslands on Marion Island varies considerably, although *P. cookii* always retains its prominence. Huntley's estimate is based upon a virtually pure stand of 30 cm high tussocks of this grass, which are typical of steeply sloping, well-drained, sea-facing slopes of the shore region and which are usually heavily influenced by animals. In these areas the ground between the tussocks is only sparsely vegetated by small coprophilous species such as *Callitriche antarctica* Engelm. ex Hegelmeyer. In contrast, inland stands of *P. cookii* tussock grassland are codominated by *Acaena magellanica* which occurs in abundance between the grass tussocks (Fig. 6). A well-developed bryophyte stratum also occurs under this *Acaena* canopy. Although numerous burrows of small petrel and prion species undermine these inland areas, damage due to trampling is minimal and no bare ground occurs between the grass tussocks. The greater vegetation cover of the inland tussock grassland communities, added to the fact that the mature grass tussocks are 40–50 cm high, accounts for the disparity between the aerial biomass value for Marion Island tussock grassland reported by Huntley (1972a) and that of the current investigation.

The vascular above-ground biomass of the taller (1 1,5 m) *Poa foliosa* tussocks on Macquarie Island (Table 5) is substantially higher than that of the smaller *P. cookii* tussocks on Marion Island but it is noteworthy that, similar to the Marion

Island tussock grasslands, those of Macquarie Island do not rely solely upon tussocks of *Poa* for their high aerial biomass values. *Stilbocarpa polaris* A. Grey is codominant with the grass in many of these areas (Taylor, 1955; Jenkin and Ashton, 1970) and the large leaves of this plant add substantially to the aerial biomass of the vegetation.

(b) *The mire complex*

The occurrence of only small amounts of living and dead vascular plant material in mire areas causes the vegetation of these areas to exhibit a low total standing crop compared with those of the slope communities (Table 4). The standing crop estimate included in the table for this vegetation does not include the algal mats which occur on the surfaces of the wetter mire areas. Dry weights of up to 500 g m^{-2} have been reported for these mats (Croome, 1973) but as they typically occupy less than 1% of the total mire surface (Table 2 and Croome, *l.c.*) they do not contribute significantly to the overall standing crop of the mire vegetation.

The above-ground biomass value of the mire vegetation agrees closely with that presented by Huntley (1972a) (Table 5) and is similar to that of graminoid-dominated swamps and clearings in the sub-Arctic of Swedish Lappland (Pearsall and Newbould, 1957) but is higher than that of alpine meadows (Bliss, 1962) due to the importance of bryophytes in the island mires. This importance is further demonstrated by the fact that the mires, although occupied by an open, low-growing vascular plant cover, support a higher biomass and total standing crop of vegetation than does a prairie grassland consisting of mixed, tall-grass species which exhibited the highest maximum above-ground biomass and standing crop (Table 5) of all those investigated in the United States IBP Grassland Biome Study (Sims and Singh, 1971). Huntley (1972a) states that a mire community on Marion Island, with only 35% aerial vascular plant cover and 15 cm in height, has a higher aerial biomass than that of many tropical grasslands.

(c) *The fjaeldmark vegetation*

The lowest above-ground biomass (and below-ground standing crop) values of all the plant communities are exhibited by the fjaeldmark vegetation (Table 4). Total standing crops of mire and fjaeldmark communities are, however, approximately equal because of large amounts of dead plant material in the *Azorella selago* cushions of the latter. True fjaeldmark, or wind desert, communities support much lower amounts of plant organic matter due to increased environmental adversity and decreased plant cover. As indicated previously, relatively well-vegetated fjaeldmark vegetation, rather than wind desert, is more representative of the rocky plateaux and ridges of the low-lying island areas.

(d) *Comparison of the standing crop of Marion Island vegetation with those of northern circumpolar tundra and alpine vegetations* (Table 5)

Fernbrake, open scrub, fjaeldmark and mire communities occupy 98% of the black lava flows of the island's eastern coastal plain and account for approximately 97% of the total vegetation standing crop of this area. Thus, despite their high standing crops, the grassland and drainage line communities do not contribute markedly to the overall vegetation.

The above-ground biomass of vascular plants in the island vegetation (306 g m^{-2}) is approximately one third greater than those of mosaic and hillocky tundra areas consisting of sedges, mosses, lichens and dwarf shrubs of the U.S.S.R. low Arctic and sub-Arctic and is four times greater than that of the Devon Island (Canadian Northwestern Territories) Truelove Lowland. The average aerial biomasses of sub-Arctic grassland and sedge-swamp communities in Swedish Lappland are also lower than that of the island vegetation. Compared with these northern tundras, however, a low (84 g m^{-2}) biomass of cryptogams occurs in the island vegetation, reflecting the relative importance in this vegetation of plant communities which do not support a significant bryophyte growth. Because of this low cryptogam component the total above-ground biomass of the island vegetation is lower than those of the sub-Arctic and low-Arctic areas.

Large amounts (over 1 100 g m^{-2}) of above-ground dead plant material accumulate in the island vegetation, thus the above-ground standing crop (approx. 1 500 g m^{-2}) is substantially higher than those of comparable low-growing sub-Arctic and low-Arctic tundra vegetations (870–1 000 g m^{-2}). Extensive sub-Arctic areas in Canada and the U.S.S.R. are occupied by a shrub tundra consisting of a tall (up to 1 m) cover of woody shrubs (mainly *Betula* and *Salix* species) understoreyed by a dense cover of cotton grass tussocks, other sedges, forbs, dwarf shrub-heaths and mosses. This vegetation exhibits extremely high standing crop and aerial biomass values, approx. 2–3 times those of the Marion Island and other circumpolar tundra-type vegetations and greater even than those of many tropical savannahs.

Alpine shrub and meadow communities exhibit much lower above-ground biomass and standing crop values than occur in the island vegetation although a maximum biomass value of 348 g m^{-2} at one site on Mt Wyoming is reported (Scott and Billings, 1964), corresponding to an approximate above-ground standing crop of 1 038 g m^{-2} (calculated by Dennis and Johnson, 1970, from the data of Scott and Billings, *l.c.*). This latter figure is roughly 40% lower than the overall vegetation standing crop on Marion Island. More than half of all sites investigated on Mt Wyoming, however, supported less than 200 g m^{-2} of live material above-ground, while estimates from Mt Washington alpine tundra range between 81 and 208 g m^{-2} (Bliss, 1962).

In contrast to the high above-ground standing crop the island vegetation contains far lower amounts of below-ground plant matter than do typical sub-Arctic low-shrub tundra vegetations. Low-Arctic tundras of sedges, mosses, lichens and shrubs, which exhibit low above-ground standing crops, possess below-ground standing crops comparable to that of the island vegetation. This accords with similar observations on South Georgia (Greene, *et al.*, 1973) and on

Signy Island (Edwards, 1973) and supports Bliss's statement (Bliss, 1970) that the Arctic environment is relatively more severe for the above- than the below-ground parts of plants and that although annual below-ground production is lower in the Arctic than in more temperate regions, the roots live longer and decompose more slowly. This longer root life, coupled with a slower decomposition rate, means that the below-ground vegetation standing crops in the cold soils of northern circumpolar regions are often higher than in the warmer (and wetter) soils of Marion Island. Even in an Arctic tundra vegetation at Barrow, Alaska, which exhibits very low above-ground standing crops (112–266 g m^{-2}), the amount of plant material below-ground (1 520–2 185 g m^{-2}) is comparable to that of the island vegetation. Dennis and Johnson (1970) suggest that the subsurface standing crop at Barrow is large because there is almost no intervening above-ground woody tissues to act as a sink for excess photosynthates and that the root systems of the plants therefore act as such a sink.

The below-ground standing crop of alpine vegetation is lower than that of Marion Island and other tundra vegetations (Table 5) although a maximum for alpine vegetation of 3 634 g m^{-2} is reported on Mt Washington (Bliss, 1966).

3. *Nutrient status of the vegetation*

(a) *Chemical composition of Marion Island plant species*

It has been indicated (Table 2 and previous sections) that five vascular plant species are responsible for the bulk of the plant cover and overall standing crop of the island vegetation. The contents of mineral elements in the leaves, leaf litter and roots (or rhizomes) of these species are presented in Table 6. Also included are the mineral element contents of fronds of the moss *Brachythecium rutabulum*.

In common with other herbaceous plant species the most prominent ash element in the living portions of Marion Island plants is potassium. The nitrogen content in the leaves and roots is commonly less than twice the potassium content, in contrast to tundra plant species of the northern hemisphere in which the concentration of nitrogen is normally considerably higher (from three to ten times) than that of any ash element (Rodin and Bazilevich, 1967).

The contents of calcium in the island plants are low compared with those of most northern hemisphere tundra plant species (Rodin and Bazilevich, *l.c.*), reflecting the low calcium status of the island soils. The calcium content of *Acaena magellanica* leaves is higher than those of the other island plants indicating a greater requirement for this element by this species and partly explaining its luxuriant growth in the relatively calcium-rich soils under drainage-line communities (Table 3). *Acaena* plants occurring in drainage lines possess greater concentrations of calcium than do those growing in the other island plant communities (Smith, 1976), suggesting a calcium deficiency in the island soils.

The island plants possess high magnesium contents, a response to both the low soil calcium status and to influx of magnesium from the surrounding ocean. Very

TABLE 6

Concentrations of mineral elements (% of dry weight) in Marion Island plant species.

Species	Organ	N	Calcium	Magnesium	Sodium	Potassium	Iron	Nitrogen	Phosphorus
Blechnum penna-marina	leaf	15	0,43±0,038	0,70±0,023	0,27±0,050	1,50±0,087	0,004±0,001	2,47±0,130	0,25±0,015
	litter	15	0,81±0,087	0,89±0,020	0,12±0,025	0,21±0,025	0,018±0,005	1,88±0,101	0,19±0,012
	rhizome	10	0,33±0,020	0,39±0,041	0,17±0,052	0,93±0,157	0,023±0,010	1,32±0,147	0,25±0,065
Acaena magellanica	leaf	8	0,70±0,070	0,52±0,043	0,42±0,063	1,39±0,201	0,015±0,008	2,03±0,101	0,23±0,016
	litter	8	0,91±0,133	0,54±0,028	0,16±0,034	0,35±0,057	0,030±0,018	2,00±0,190	0,18±0,013
	root	8	0,19±0,029	0,24±0,037	0,08±0,045	0,57±0,043	0,021±0,018	0,95±0,041	0,12±0,021
Poa cookii	leaf	12	0,12±0,013	0,08±0,010	0,26±0,053	1,26±0,105	0,009±0,005	1,69±0,123	0,16±0,010
	litter	8	0,15±0,049	0,11±0,012	0,09±0,031	0,15±0,070	0,024±0,010	1,15±0,144	0,11±0,018
	root	7	0,14±0,044	0,13±0,026	0,25±0,071	0,43±0,053	0,075±0,005	1,22±0,121	0,11±0,017
Azorella selago	leaf	12	0,47±0,073	0,33±0,048	0,88±0,140	1,47±0,211	0,018±0,005	1,47±0,127	0,14±0,011
	litter	12	0,55±0,041	0,30±0,049	0,04±0,019	0,08±0,013	0,114±0,055	1,11±0,101	0,10±0,014
	root	8	0,42±0,063	0,38±0,036	0,18±0,034	0,87±0,103	0,017±0,005	1,35±0,035	0,14±0,013
Agrostis magellanica	leaf	4	0,13±0,030	0,19±0,023	0,45±0,374	1,01±0,517	0,007±0,003	1,90±0,891	0,16±0,071
	litter	4	0,16±0,056	0,14±0,015	0,12±0,062	0,18±0,214	0,022±0,011	0,95±0,279	0,08±0,038
	root	2	0,22±0,307	0,28±0,180	0,27±0,266	0,51±0,438	N.D.	0,86±0,457	0,17±0,321
Brachythecium rutabulum	living frond	7	0,39±0,103	0,36±0,037	0,13±0,035	0,83±0,041	0,045±0,020	1,81±0,136	0,17±0,044

Values expressed as means ± 95% confidence limits
N = number of samples
N.D. = not determined

heavy influx of sodium also occurs from this source and the plants characteristically contain high concentrations of this element. As demonstrated in Table 6, the concentration of sodium is second only to that of potassium amongst the ash elements in leaves of *Azorella selago*, *Poa cookii* and *Agrostis magellanica*. This is also true for the leaves of at least four other island plant species, *Montia fontana* L., *Uncinia dikei*, *Juncus scheuchzerioides* and *Agrostis* sp. cf. *A. antarctica* (preliminary, unpublished data). Both *A. selago* and *P. cookii* often form an important component of the vegetation in areas heavily influenced by wind-whipped salt-spray and occasional inundation by waves. Their salt tolerance may be related to an ability to tolerate high internal levels of sodium before suffering injury.

Although the exchangeable sodium status of the mire peat is low (Table 3) this is due to the inherently low retention capacity of colloidal active surfaces for the sodium ion. Proportionately, salt-spray has virtually the same ionic composition as sea-water (Malloch, 1972; Grobbelaar, 1975) and however slight the deposition of this salt-spray on the mire surfaces, because of the slow drainage from these areas, the mire soil solution can be expected to contain relatively higher proportions of sodium than of any other cation. This is substantiated by unpublished data (Grobbelaar, 1975, D.Sc. manuscript) on the ionic concentration of the island's soil solutions. Intensive leaching of sodium from surrounding slope areas also enriches the mire soil water in this element. It is likely, therefore, that the high sodium contents of the leaves of plants occurring predominantly in mire areas *(Agrostis magellanica, J. scheuchzerioides, U. dikei* and *M. fontana)* reflect the disproportionately high sodium concentration in the soil solution and may represent an adaptation enabling these plants to exploit the otherwise nutrient-poor mire substrate.

The mineral element content of the leaf litter of most island plant species differs from that of the corresponding leaf tissue in that there is a relative increase in calcium, magnesium and iron whereas there is an absolute decrease in the more mobile elements such as sodium, potassium, nitrogen and phosphorus (Table 6). The higher calcium and magnesium contents in the litter are most likely caused by the withdrawal of photosynthates from dying leaves resulting in a decrease in the dry weights of these leaves rather than to intrinsic increases in the amounts of the two elements in the actual dead leaf material.

Because the mire substrate is poor in available nutrients, the amounts of elements reabsorbed before leaf-death or leaf-fall may be critical to the success of plant species growing under the waterlogged, nutrient-deficient mire conditions. In this context it is of interest to note that the data in Table 6 indicates a greater reabsorption of sodium, nitrogen and phosphorus from dying leaves of *Agrostis magellanica* than from those of the other, non-mire, plant species, supporting the proposal (Small, 1972a; 1972b) that bog species subsist on relatively smaller amounts of nutrients than do plants in other habitats and that this is related to the ability of the bog species to reabsorb a greater proportion of the nutrients from their leaves preceding leaf-fall than do non-bog species.

On Marion Island approximately 50% of *Acaena magellanica* leaf material which had senesced and died early in March 1974 was lost through decomposition by the first week in May of that year. Greene, *et al.* (1973) states that the decay of *Acaena* leaves on South Georgia is so rapid that over 90% of the litter is lost in three months as compared with a 25% loss in one year for *Festuca erecta* litter. At senescence there is an especially rapid decrease in the dry weights of *Acaena* leaves as the leaf carbohydrates are incorporated into the extensive perennial roots and stems of the plants. This decrease in leaf dry weight masks simultaneous losses of leaf nitrogen so that the resultant litter indicates the same nitrogen content per unit dry weight as does the living tissue. This high nitrogen content in *Acaena* leaf litter may be partly responsible for the observed rapid rates of decay of this material in the field.

TABLE 7.

Amounts of ash elements plus nitrogen (g m^{-2}) contained in the plant matter of the Marion Island plant communities.

Community		Above-ground				Total Above	Below-ground Total	Total in S.C.
		Biomass Vasc.	Cryp.	Total	Dead O.M.			
Fernbrake	Ash elements	16,47		16,47	24,90	41,37	74,67	116,04
	N	11,48		11,48	20,76	32,24	52,17	84,41
	Ash elements + N	27,95		27,95	45,66	73,61	126,84	200,45
Open scrub	Ash elements	13,06		13,06	21,22	34,28	42,89	77,17
	N	7,96		7,96	19,25	27,21	30,88	58,09
	Ash elements + N	21,02		21,02	40,47	61,49	73,77	135,26
Drainage Line	Ash elements	20,66	4,13	24,79	11,26	36,05	34,20	70,25
	N	13,30	3,83	17,13	9,70	26,83	26,25	53,08
	Ash elements + N	33,96	7,96	41,92	20,96	62,88	60,45	123,33
Slope Crest	Ash elements	17,97		17,97	34,97	52,94	28,74	81,68
	N	12,32		12,32	38,13	50,45	25,66	76,11
	Ash elements + N	30,29		30,29	73,10	103,39	54,41	157,80
Tussock grassland	Ash elements	21,98	4,66	26,64	21,00	47,64	52,22	99,86
	N	15,38	4,46	19,84	25,42	45,26	43,88	89,14
	Ash elements + N	37,36	9,12	46,48	46,42	92,90	96,10	189,00
Mire	Ash elements	2,29	5,94	8,23	2,07	10,30	29,35	39,65
	N	2,24	5,49	7,73	2,80	10,53	17,40	27,93
	Ash elements + N	4,53	11,43	15,96	4,87	20,83	46,75	67,58
Fjaeldmark	Ash elements	7,07		7,07	18,74	25,81	18,39	44,20
	N	3,76		3,76	16,21	19,97	12,23	32,20
	Ash elements + N	10,83		10,83	34,95	45,78	30,62	76,24

(b) *Contents of mineral elements in the standing crop components of the various plant communities*

The amounts of ash elements plus nitrogen contained in the vegetation of the various island plant communities are presented in Table 7. In general, these amounts are approximately proportional to the standing crops of the respective communities. A disproportionately large amount of mineral elements is found in the fernbrake community, however, due to the high proportion of living green tissue (leaves of *Blechnum penna-marina*) in the standing crop of this community.

In proportion to their high standing crops, tussock grassland and slope-crest communities contain relatively low amounts of mineral elements. This is due to the importance of *Poa cookii* and *Azorella selago* leaf litter in the above-ground standing crop component and not to inherently low concentrations of mineral elements in the plants of the two communities. Smith (1976) has shown that most plants occurring in the tussock grassland community are in fact richer in nitrogen, phosphorus, potassium and iron than are plants of the same species occurring in the other plant communities.

Mire vegetation also contains a low amount of mineral elements in proportion to the standing crop, despite the fact that this vegetation consists wholly of graminoid and bryophyte species and that no perennial or non-green living tissue occurs in the above-ground component of the standing crop. Seventy-six per cent of the plant material in mire communities occurs below ground compared with corresponding values of 31–71% for the other island plant communities. This greater importance of the below-ground component, as well as low concentrations of mineral elements in the litter of mire-plant species (see previous section) is responsible for the low amounts of mineral elements contained in the standing crop of mire communities.

TABLE 8.

Amounts of mineral elements (kg ha^{-1}) contained in the standing crop components of Marion Island vegetation.

Element	Above-ground				Total Above	Below-ground Total	Total in S.C.
	Biomass Vasc.	Biomass Cryp.	Biomass Total	Dead O.M.			
Calcium	12,06	5,13	17,19	59,13	76,32	65,55	141,87
Magnesium	12,60	4,26	16,86	43,75	60,61	74,92	135,53
Sodium	15,86	1,23	17,09	8,35	25,44	49,09	74,53
Potassium	38,40	9,90	48,30	13,83	62,13	149,38	211,51
Iron	0,26	0,39	0,65	5,34	5,99	4,16	10,15
Phosphorus	5,70	1,72	7,42	12,08	19,50	39,18	58,68
Total ash elements	84,88	22,63	107,51	142,48	249,99	382,28	632,27
Nitrogen	56,65	19,92	76,57	128,93	205,50	257,24	462,74
Total mineral elements	141,53	42,55	184,08	271,41	455,49	639,52	1 095,01

(c) *Overall standing crop of mineral elements in the island vegetation*

The amounts of mineral elements contained in the vegetation standing crop of an average hectare of the island's low altitude black lava areas are presented in Table 8.

Because of the prominence of herbaceous and moss species in the island vegetation and in accordance with the data presented in Table 6 there is a predominance of potassium amongst the ash elements of this vegetation, despite substantial accumulation of calcium and magnesium in the dead, above-ground plant matter.

A total content of 1 095 kg ha^{-1} of mineral elements accumulates in the plant matter of the island's low altitude terrestrial vegetation, 42% of which is attributable to nitrogen. This value is low compared with many northern hemisphere shrub tundras where, because of high below-ground standing crops, similar amounts of mineral elements may accumulate in the biomass component of the vegetation alone (Rodin and Bazilevich, 1968).

Whereas in typical shrub tundra vegetation the bulk (80%) of mineral elements is contained in the below-ground sphere (Rodin and Bazilevich, 1967) only 58% of the mineral elements incorporated in the island vegetation are located below ground. This is due to the relatively low below-ground standing crop of this vegetation and to the accumulation of sodium, magnesium and potassium in the above-ground plant organs due to influx of these metals from the surrounding ocean.

CONCLUSION

Marion Island is situated at a much lower latitude than are any of the northern circumpolar areas represented in Table 5. In addition, the moderating influence of the ocean dominates the island's climate, keeping the temperature fairly constant throughout the year (Table 1) and preventing the occurrence of bitterly cold weather. The length of the growing season and the air and soil temperature regimes on the island are consequently more conducive towards plant growth than are those of northern circumpolar tundra regions possessing a continental climate without the dampened seasonal effect of a surrounding ocean. In contrast to most of these circumpolar areas where permafrost is common and unfrozen soil water available for only a restricted period during the year, the soils of Marion Island have a plentiful water supply. In addition, these soils are highly organic and are deep and fine-textured, edaphic conditions favouring the development of maximum above-ground standing crops in alpine vegetation (Scott and Billings, 1964) and in sub-Arctic tundra (Pearsall and Newbould, 1957; Gorham, 1974).

These more favourable conditions for plant growth are reflected in the accumulation of large quantities of alive and dead above-ground vascular plant material in the Marion Island vegetation and cause the above-ground standing crop of this vegetation to be higher than that of comparable low-growing sub-Arctic and low

Arctic tundra vegetations despite the much higher biomass of cryptogams in the latter. This confirms previous observations that the above-ground standing crops of low altitude sub-Antarctic vegetations are higher than those of most other comparable northern hemisphere tundra vegetation types (Jenkin and Ashton, 1970; Huntley, 1972a; Wielgolaski, 1972a, 1972b; Green, *et al.*, 1973; Walton, 1973).

Although the high above-ground biomass of vascular plants on Marion and other sub-Antarctic islands indicates that environmental stresses are less severe on sub-Antarctic plant communities than on northern circumpolar tundra and alpine plant communities, it is not at present certain why such high above-ground standing crops develop in the vegetation of sub-Antarctic regions as compared with those of temperate and tropical grasslands. In addition to the long preservation of above-ground plant remains, Jenkin and Ashton (1970) postulate that the luxuriance of Macquarie Island grasslands is related to a long growing season, a relatively depressed temperature optimum for the plant species and a prolonged leaf longevity. On Marion Island the virtual absence of herbivores must play an important role in the development of the high standing crop of the lowland plant communities (Huntley, 1972a).

The predominance of green material and the *halophytic* nature of the island vegetation causes the above-ground biomass component of this vegetation to contain a disproportionately large amount of ash elements compared to most other tundra vegetation types. As indicated in Rodin and Bazilevich (1967) halophytic communities may accumulate very high values of chemical elements in their biomass, especially if this biomass is fairly large. The importance of the surrounding ocean on the accumulation of mineral elements by the island vegetation is demonstrated by the fact that 136 kg of mineral elements (including silica, manganese and aluminium) are contained in an above-ground biomass of 4 900 kg ha^{-1} of a U.S.S.R. low-Arctic shrub tundra whereas the smaller biomass (3 900 kg ha^{-1}) of the island vegetation incorporates 184 kg of mineral elements, excluding the content of silica, manganese and aluminium (Rodin and Bazilevich, *l.c.*).

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